

Infrared Warming Affects Intrarow Soil Carbon Dioxide Efflux during Vegetative Growth of Spring Wheat

Gerard W. Wall,* Jean E. T. McLain, Bruce A. Kimball, Jeffrey W. White, Michael J. Ottman, and Richard L. Garcia

ABSTRACT

Global warming will likely affect carbon cycles in agricultural soils. Our objective was to deploy infrared (IR) warming to characterize the effect of global warming on soil temperature (T_s), volumetric soil-water content (θ_s), and intrarow soil CO_2 efflux (Φ_s) of an open-field spring wheat (*Triticum aestivum* L. cv. Yecora Rojo) crop grown in the semiarid desert Southwest. A temperature free-air controlled enhancement (T-FACE) apparatus using IR heaters maintained canopy air temperature above 3.0-m plots by 1.3 and 2.7°C (0.2 and 0.3°C below the targeted set-points) during the diurnal and nocturnal periods, respectively. A randomized complete block (RCB) design with two IR warming treatments (i.e., Heated; Reference) in three replicates was planted on 10 Mar. and 1 Dec. 2008. Intrarow T_s , θ_s , and Φ_s were measured from emergence (bare soil) up until inflorescence emergence (canopy closure). Under ample soil water supply with high θ_s , midday Φ_s was 10% greater in Heated [$4.1 \mu\text{mol} (\text{CO}_2) \text{m}^{-2} \text{s}^{-1}$] compared with Reference [$3.7 \mu\text{mol} (\text{CO}_2) \text{m}^{-2} \text{s}^{-1}$]. In contrast, as the soil dried and θ_s decreased to a greater degree in Heated compared with Reference, a 10% decrease in Φ_s occurred in Heated compared with Reference. Overall, θ_s had the greatest impact on Φ_s , whereas it was responsive to T_s only under high θ_s . Accurate predictions of global climate change effects on Φ_s in agricultural soils require that interactive effects of T_s and θ_s be coupled. Infrared warming with T-FACE proved to be an effective experimental methodology to investigate these interactive effects.

SOILS IN TERRESTRIAL ecosystems contain 1550 Pg of carbon (Eswaran et al., 1993; Hibbard et al., 2005). Compared with gross primary production, soils provide the second largest exchange of carbon between terrestrial ecosystems and the atmosphere at 68 to 80 Pg (C) yr^{-1} (Raich and Schlesinger, 1992; Raich and Potter, 1995; Raich et al., 2002; Schlesinger and Andrews, 2000). Because soils are an important source or sink of carbon, they are a primary determinant of net ecosystem carbon balance, and they provide seasonal and interannual feedback control on atmospheric CO_2 concentration (Taylor and Lloyd, 1992; Raich et al., 2002). An increase in carbon influx from atmosphere to soil (e.g., sequestration) could mitigate the effect of atmospheric CO_2 concentration and reduce global warming (negative feedback), whereas an increase in carbon efflux from soil to atmosphere (e.g., autotrophic and heterotrophic soil respiration) could intensify global warming (positive feedback) (Rustad et al., 2001; Melillo et al., 2002).

Any change in Φ_s because of either thermal acclimation of the soil, substrate depletion of soil organic matter, or soil dehydration in response to warmer global temperatures could affect the direction and magnitude of any feedback between the terrestrial carbon cycle and global climate change in semiarid desert regions of the Earth.

Soil CO_2 efflux represents the net of total belowground carbon metabolism (Raich and Nadelhoffer, 1989; Schlesinger and Andrews, 2000). Biotic factors account for approximately one-half of Φ_s (Hanson et al., 2000; Bond-Lamberty et al., 2004; Subke et al., 2006; Schindlbacher et al., 2009). They include autotrophic respiration from rhizosphere microbes and plant roots and heterotrophic respiration from microbial decomposition of litter and soil organic matter (Hanson et al., 2000; Wan and Luo, 2003; Kuzyakov, 2006; Subke et al., 2006), and the dynamics of these microbial communities (Rustad et al., 2000, 2001; Melillo et al., 2002; Singh et al., 2009). Abiotic factors affecting Φ_s include atmospheric

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Abbreviations: DOE, day of experiment; df_1 , first degrees of freedom for the F -statistic; df_2 , second degrees of freedom for the F -statistic; e_a , air water vapor pressure (kPa) at T_a ; e_a^* , saturation water vapor pressure at T_a ; $e_{a,VPD}$, atmospheric water vapor pressure deficit (i.e., $e_a^* - e_a$) at T_a (kPa); F , F -statistic; HSC, Hot Serial Cereal; IR, infrared radiation (W m^{-2}); P , probability of a greater F -statistic by chance; RCB, randomized complete block experimental design; REP, replication effect in analysis of variance; RTV, repeated measure time variant effect in analysis of variance; T_a , ambient air temperature (°C); $T_{a,max}$, maximum T_a (°C); $T_{a,min}$, minimum T_a (°C); T_s , soil temperature (°C); $T_{s,max}$, maximum T_s (°C); $T_{s,min}$, minimum T_s (°C); T-FACE, infrared-based temperature free-air controlled enhancement; TOD, time of day effect in analysis of variance; TRT, infrared warming effect in analysis of variance; SR, daily solar radiation ($\text{MJ m}^{-2} \text{d}^{-1}$); θ_s , volumetric soil-water content (v/v); Φ_s , intrarow soil carbon dioxide efflux [$\mu\text{mol} (\text{CO}_2) \text{m}^{-2} \text{s}^{-1}$]; u_a , air wind speed at 2-m height (m s^{-1}); $u_{a,avg}$, daily average air wind speed at 2-m height (m s^{-1}).

CO₂ concentration, nutrient availability (Raich and Tufekcioglu, 2000) - particularly N (Hungate et al., 2009), soil physical properties (Moyano et al., 2012), substrate from rhizodeposition (Hütsch et al., 2002), temperature (Lloyd and Taylor, 1994; Boone et al., 1998; Rustad et al., 2001; Fang and Moncrieff, 2001; Hartley et al., 2007a), and water (Davidson et al., 2000; Fierer and Schimel, 2002, 2003; Liu et al., 2002; Conant et al., 2004; Harper et al., 2005; Shen et al., 2008). Any abrupt perturbations in any of these biotic and abiotic factors are known to strongly impact Φ_s (Shen et al., 2009).

Global mean surface air temperature (T_a) is warming (IPCC, 2007), which could alter the microclimate at the soil–air interface and strongly impact Φ_s . A possible consequence of increased T_a will be a change in carbon cycles including sequestration (influx of carbon) and soil respiration (efflux of carbon) processes in agricultural soils. Soil CO₂ efflux is highly sensitive to changes in T_s and has been characterized as exponential with a Q_{10} temperature response – the factor by which Φ_s differs for a temperature interval of 10°C (Fang and Moncrieff, 2001). The lowest Q_{10} has been observed in warm dry semiarid desert regions, which contain low soil organic matter, whereas the highest Q_{10} occurs in cool wet tundra ecosystems, which contain high soil organic matter (Zhou et al., 2009). Undoubtedly, the effect of changing climate on temperature and precipitation will exert controls on Φ_s (Davidson et al., 1998). As such, relatively small changes in T_a may possibly have a profound influence in the direction and magnitude of the response in Φ_s . Consequently, any global-warming-induced increase in Φ_s from agricultural soils may possibly have a lesser or greater positive (efflux of carbon) feed-forward effect on the atmospheric CO₂ concentration and global warming (Kirschbaum, 1995, 2000).

A non-invasive, cost-effective method to conduct ecosystem warming experiments in situ has been developed using IR heaters (Kimball et al., 2008). Infrared warming experiments have been conducted on natural and rangeland ecosystems (Harte and Shaw, 1995; Harte et al., 1995; Parton et al., 2007; Kimball et al., 2008; Niu et al., 2008; Wan et al., 2009; Xia et al., 2009; Luo et al., 2010; Morgan et al., 2011), as well as agricultural crop production systems (Kimball et al., 2008; Wall et al., 2011). Infrared warming has induced earlier spring snow-melt and impacted the thermal regimes of the air and soil, and soil moisture (Harte and Shaw, 1995; Harte et al., 1995; Nijs et al., 1996; Wan et al., 2002). In addition, IR warming and consequent soil drying have been shown to alter the soil mesofauna (Harte and Shaw, 1995; Harte et al., 1995; McLain et al., 2009), increase soil N mineralization rates (Shaw and Harte, 2001), alter soil respiration rates (Luo et al., 2001), alter methanotroph activity and methane fluxes in the soil (Torn and Harte, 1996), and decrease whole-ecosystem CO₂ flux (Saleska et al., 1999).

Our objectives were to investigate the feasibility of the IR warming approach with a T-FACE apparatus as an effective methodology to investigate the impact of global warming on Φ_s in an agricultural soil, and to characterize and quantify any IR warming effect on T_s , θ_s , and intrarow Φ_s in a hard red spring wheat (*T. aestivum* L.) crop grown in an agricultural field. Because IR warming can alter the microclimate of

experimental plots (Harte and Shaw, 1995; Nijs et al., 1996; Wan et al., 2002; Wall et al., 2011), to test the hypothesis that an in situ IR warming apparatus used in conjunction with supplemental irrigation will still alter the microclimate within the intrarow space of a wheat crop (Hypothesis 1), comparisons of T_s and θ_s were made between IR-warmed (Heated) and non-warmed (Reference) plots. An increase in Φ_s with an increase in temperature is generally true for a short period of warming, but it will usually decrease after soil water feedback occurs. Consequently, to test the hypothesis that Φ_s will increase as T_s increases at high θ_s , but that any IR-warming-based thermal response on Φ_s will diminish at low θ_s as the soil dries, comparisons of Φ_s were made between Heated and Reference plots at high θ_s after an irrigation or precipitation event and at low θ_s as the soil dried (Hypothesis 2).

MATERIALS AND METHODS

Study Region and Experimental Design

A detailed description of the study region, crop culture, IR warming apparatus (Kimball, 2005; Kimball et al., 2008), surface drip irrigation system (including supplemental irrigation), and experimental design has been provided elsewhere (Wall et al., 2011). Briefly, the experiment site was located in a semiarid desert region of the Southwest at the University of Arizona's Maricopa Agricultural Center (MAC), Maricopa, AZ (33.07° N, 111.97° W; 361 m above sea level). The soil was a Trix clay loam (fine-loamy, mixed [calcareous] hyperthermic Typic Torrifluent) with low soil organic matter content (~1.2%) in the upper 0.15 m of the soil profile. Use of a homogeneous cultivated agricultural soil minimized spatial variability in Φ_s within the field site. Soil fertility was managed to avoid nutrient limitations. Except for the use of drip rather than flood irrigation, all other agronomic activities were in accordance with local recommended practices.

As a component of a larger Hot Serial Cereal (HSC) experiment (Wall et al., 2011) plantings occurred on 10 Mar. 2008 (day of experiment [DOE] 364) and 1 Dec. 2008 (DOE 630), which corresponded to the 9th and 14th of a total of 15 plantings in the HSC experiment (Fig. 1g, 1h; also see Supplemental Table 1, Wall et al., 2011). Certified wheat (cv. Yecora Rojo) seeds were sown in three replicates (i.e., $n = 3$) of three treatments (i.e., Control, Reference with dummy heaters, Heated) in a 3 by 3 Latin square experimental design on flat ground in north–south rows, 0.19 m-apart, with a grain drill. The wheat was planted in blocks 11 m on a side separated by 1.2 m alleyways for a total of approximately 57 rows per plot. The sample area was circular (3-m diam.) and centered within each plot (Ottman et al., 2012). Seeding rates were 134 kg seed ha⁻¹ (288 seeds m⁻²). Soil CO₂ efflux sampling dates for Heated and Reference plots are designated in Fig. 1g and 1h.

Soil Temperature and Volumetric Soil-Water Content Measurements and Meteorological Conditions

Soil temperature at the 0.1-m depth was measured using a thermocouple probe (LI-8100-201; LI-COR Biosciences, Lincoln, NE) connected to a portable automated CO₂ soil flux system (LI-8100A) on 17 Dec. 2008 through 2 Mar.

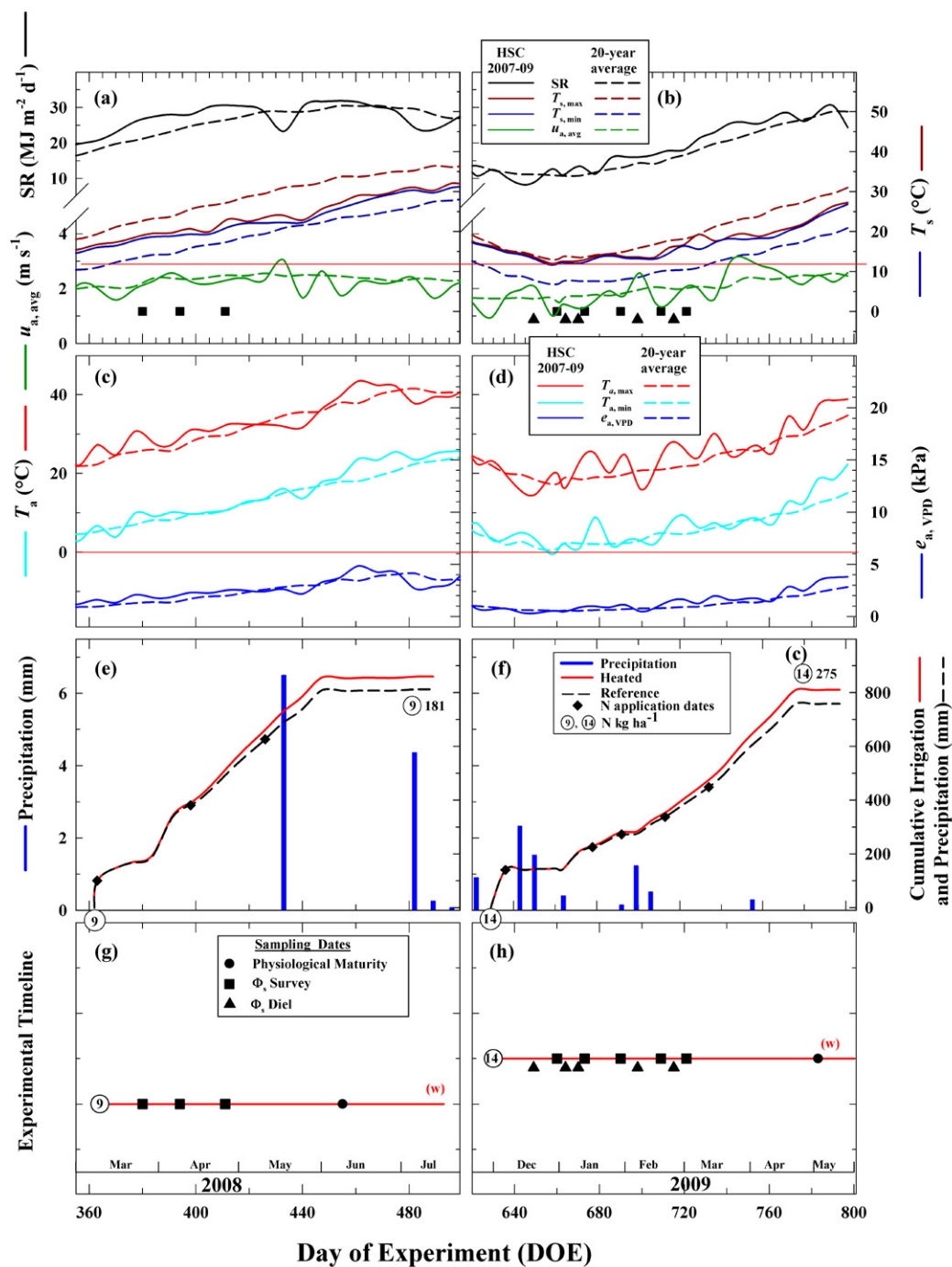


Fig. 1. (a, b, c, d) Average meteorological conditions over a 20-yr period (1987–2007) before and during (2007–2009) the Hot Serial Cereal (HSC) experiment at Maricopa, AZ (33.07° N, 111.97° W; 361 m above sea level) – a semiarid desert region of the Southwest. (a, b) Mean daily solar radiation (SR), maximum ($T_{s,max}$) and minimum ($T_{s,min}$) soil temperatures (T_s), daily average wind speed of the air ($u_{a,avg}$) at 2-m height, and sampling dates for microclimate measurements of T_s , volumetric soil-water content (θ_s), and soil CO_2 efflux (Φ_s) for midday survey (filled square) and unattended diel (24 h) (filled triangle) periods. (c, d) Mean daily maximum ($T_{a,max}$) and minimum ($T_{a,min}$) air temperatures (T_a), and daily vapor pressure deficit ($e_{a,vpd}$). (e, f) Rainfall events and amounts, cumulative irrigation plus rainfall amounts for Heated and Reference plots (e.g., note that Heated plots received supplemental irrigations that provided 10% more soil-water than Reference plots to provide a first-order correction for any increase air-to-plant vapor pressure [Kimball, 2005]), and N application dates (filled diamond) and amounts (e.g., note that the first N application date actually designates date of initial irrigation to germinate seeds [see Supplemental Table 1; Wall et al., 2011]) for Heated and Reference plots. (g, h) Timeline of planting scheme for HSC experiment denoting 9th and 14th plantings of the wheat crop grown in a cooler-to-warmer (designated with [w] in red as a warming trend) thermal regime. The physiological maturity date of the wheat crop is denoted (filled circle), whereas the harvest date is denoted by the end of the red line. Calendar month and year are given as an additional x axis, which is synchronized with day of experiment (DOE).

Table 1. Analysis of variance for treatment (TRT: Reference; Heated), time of day (TOD), and TRT \times TOD interaction effects, and independent continuous covariates of meteorological (solar radiation [SR]; air temperature [T_a]; wind speed [u_a]) and soil (temperature [T_s]; volumetric soil-water content [θ_s]) effects on soil CO₂ efflux (Φ_s) during five 2-wk intervals centered on day of experiment given.

Source	df ₁	649			664†			674†			698			715		
		df ₂	P > F‡		df ₂	P > F		df ₂	P > F		df ₂	P > F		df ₂	P > F	
TRT	1	2.21	0.1650		5.74	0.0349		2.47	0.0698		21.9	<0.0001		5.59	0.0037	
TOD	23	35.3	0.1935		11.15	<0.0001		60.6	<0.0001		71.5	0.6092		89.4	<0.0001	
TRT \times TOD	23	35.3	0.3854		1.71	0.0474		60.1	0.0253		71.0	0.5532		89.4	0.3760	
T_s	1	ns§	ns		ns	ns		ns	ns		ns	ns		77.4	0.0620	
θ_s	1	ns	ns		ns	ns		6.18	0.0057		ns	ns		ns	ns	
SR	1	ns	ns		ns	ns		ns	ns		ns	ns		90.11	0.0126	
T_a	1	ns	ns		4.43	0.0512		64	<0.0001		31.4	0.0091		ns	ns	
u_a	1	ns	ns		ns	ns		44.1	0.0012		55.9	0.0289		ns	ns	

† Log₁₀ transformation of Φ_s .

‡ F is the F-statistic; df₁ is the first degrees of freedom for the F-statistic; df₂ is the second degrees of freedom for the F-statistic; and, P is the probability of a greater F-statistic by chance.

§ Stepwise deletion of nonsignificant (ns) meteorological (SR, T_a , u_a) and soil (T_s , θ_s) covariates.

2009 (DOE 649–721) during the 14th planting (Fig. 1h). Volumetric soil-water content was monitored at 0- to 0.1-m soil depth automatically using soil moisture ring capacitance probes (EnviroSMART, Sentek Sensor Technologies, Stepney, Australia) in each plot. On 13 and 30 Jan. 2009 and 18 Feb. 2009 (DOE 673, 690, and 709, respectively) θ_s was determined gravimetrically (kg kg⁻¹) for the 0- to 0.1-m soil depth. A soil bulk density of 1.38 mg mm⁻³ was used to convert gravimetric values (kg kg⁻¹) to volumetric θ_s (m³ m⁻³). Meteorological data were obtained from the MAC field site weather station (AZMET; <http://ag.arizona.edu/AZMET/06.htm>) located approximately 1 km from the experiment.

Soil Carbon Dioxide Efflux Measurements

Midday (solar noon) Φ_s was measured manually over Heated and Reference plots across three replicates (six plots) using a survey chamber (LI-8100-103) attached to a portable automated soil CO₂ flux system (LI-8100A) to characterize spatial variance (24 Mar. 2008 through 28 Apr. 2008 [DOE 380, 394, 411] during the 9th planting; 17 Dec. 2008 through 2 Mar. 2009 [DOE 649, 660, 664, 673, 674, 690, 698, 709, 715, 721] during the 14th planting; Fig. 1g, 1h). In addition, an unattended long-term chamber with a self-actuating armature (LI-8100-104), attached to a portable automated soil CO₂ flux system (LI-8100A), measured diel Φ_s every 15 min (96 measurements per 24 h period) for 10 wk (18 Dec. 2008 through 28 Feb. 2009 [DOE 649, 664, 674, 698, 715]) to characterize the temporal variance. A week of diel Φ_s measurements in a Heated plot was followed by a week of diel Φ_s measurements in a Reference plot. Three consecutive days within each week with the most similar meteorological (solar radiation [SR], T_a , wind speed at 2-m height [u_a]) and soil conditions (T_s , θ_s) between the first and second week of each 2-wk measurement interval were used to compare Φ_s between Heated and Reference plots. Hence, the 3 most similar consecutive days in a week were used as replicates. A total of five 2-wk (i.e., first week Heated plot, second week Reference plot) comparisons of diel Φ_s over a 10-wk period were made. Both survey and unattended chambers were deployed on a poly-vinyl-chloride (PVC) collar (0.05-m height protruded

above soil surface, 0.2-m inside diameter) that provided for a large enough soil area (0.0314 m²) to characterize spatial variability in measurements of Φ_s between Heated and Reference plots. A PVC collar was pressed into the soil to a depth of about 0.03 m at the center of the Φ_s measurement activity area (Ottman et al., 2012). Adequate cultivation and seedbed preparation provided a bare soil that was devoid of any aboveground vegetation or belowground living root system – devoid of any autotrophic respiration – in the intrarow space where PVC collars were installed. To minimize perturbation effects on Φ_s , PVC collars were placed in each plot at least 3 d before measurements and remained in the plots until the end of the experiment. Upon sealing the PVC collar, Φ_s was measured by monitoring the change in CO₂ concentration with an IR gas analyzer (transient technique).

Statistical Analysis

To test the main fixed TRT effect for T_s and θ_s for Hypothesis 1 (whether the Heated treatment affected T_s and θ_s ; Heated vs. Reference) across 13 midday sampling dates (DOE 380–721), a RCB (2 by 3) embedded within the 3 by 3 Latin square experimental design was used for the mixed model ANOVA (Littell et al., 1996) using the SAS Mixed Procedure (version 9.2, SAS Institute, Cary, NC) (SAS Institute, 2009). A first-order, autoregressive, moving average covariance structure was used for the fixed effect time variate (RTV) to account for correlations among repeated measures and any irregular sample intervals. The TRT \times RTV tested the interaction effect. Replication (REP) was treated as a random effect.

To test the main fixed TRT effect for Hypothesis 2 (whether the Heated treatment affected Φ_s ; Heated vs. Reference) at midday differently under high and low levels of θ_s , a RCB experimental design was used for the mixed model ANOVAs for each DOE. The REP was a random effect.

To further test the main fixed TRT effect for Φ_s for Hypothesis 2 hourly throughout a diel period, a RCB experimental design was analyzed for the mixed model ANOVAs. Each hourly time of day (TOD) over the diel period was treated as a fixed effect time variate – repeated measure similar to the analysis described above for the RTV effect on TRT and

TRT \times RTV effect conducted at midday. The 3 most similar consecutive days in a week in regards to meteorological (SR, T_a , u_a) and soil (T_s , θ_s) condition over the 2-wk sample interval were treated as a REP random effect. Five continuous independent variables that depict the influence of natural variation in meteorological (SR, T_a , u_a) and soil (T_s , θ_s) conditions on Φ_s were treated as covariates. A stepwise reduction in nondetectable covariates was conducted to minimize their effect on any tests of detectable TRT, TOD, and TRT \times TOD effects on Φ_s for Hypothesis 2.

To avoid pseudo-replication, all ANOVAs were performed on replication means. Statistical significance was reported in the text as follows: ($F_{df1, df2}$; P); where, F is the F -statistic; df_1 is the first degrees of freedom for the F -statistic; df_2 is the second degrees of freedom for the F -statistic; and, P is the probability of a greater F -statistic by chance. Tests for homogeneity of variance and subsequent data transformation were performed using residuals diagnostic plots as appropriate (Box et al., 1978). Statistical differences and least-square mean comparisons were performed for each DOE and TRT effect. Mean separation was performed with pairwise t test, equivalent to Fisher's least significant difference test.

RESULTS

Meteorological Conditions of Study Region

The 20-yr mean daily SR, maximum ($T_{s,max}$) and minimum ($T_{s,min}$) T_s at the 0.1-m soil depth and average daily u_a ($u_{a,avg}$) at 2-m height (Fig. 1a, 1b), and maximum ($T_{a,max}$) and minimum ($T_{a,min}$) T_a and average daily vapor pressure deficit ($e_{a,VPD}$) (Fig. 1c, 1d) for the 9th and 14th plantings, respectively, are illustrated in Fig. 1 (Wall et al., 2011). During the measurement interval for Φ_s , SR averaged 28.1 and 14.0 MJ m⁻² d⁻¹ ranging from 18.7 to 31.5 MJ m⁻² d⁻¹ and from 3.8 to 21.5 MJ m⁻² d⁻¹ during the 9th and 14th plantings, respectively. Wind speed averaged 2.3 and 1.7 m s⁻¹ with a maximum of 12.1 and 15.0 m s⁻¹ for the 9th and 14th plantings, respectively. The 14th planting occurred during a normal cropping period for spring wheat in Arizona (December–May; Fig. 1h), whereas the 9th planting (March–July; Fig. 1g) was 3 mo later than normal. Consequently, T_a and SR were greater during the 9th compared with the 14th planting. Nevertheless, during the sample interval when Φ_s was measured, T_a increased (i.e., cooler-to-warmer trend) during both the 9th (Fig. 1a) and 14th (Fig. 1b) plantings. During the sample interval when Φ_s was measured on the ninth planting, the average T_s at the 0.1-m soil depth was 19.5°C and ranged from $T_{s,max}$ (31.3°C) to $T_{s,min}$ (17.0°C). During the 14th planting when Φ_s was measured, the average T_s at the 0.1-m soil depth was 13.4°C and ranged from $T_{s,max}$ (19.5°C) to $T_{s,min}$ (11.5°C). Therefore, over the sample interval when Φ_s was measured the average T_s was 6.1°C warmer, and $T_{s,max}$ was warmer by 11.8°C and $T_{s,min}$ was warmer by 5.5°C during the 9th compared with the 14th planting, respectively. Despite these differences, the range in T_s over the sample interval when Φ_s was measured was characteristic of soil conditions that commonly occur from emergence (bare soil) through inflorescence emergence (canopy closure) in a spring wheat crop grown in a semiarid desert region of the Southwest.

After the initial irrigation to germinate the wheat seed on DOE 364, several irrigation events occurred, but no

precipitation fell during the sample interval when Φ_s was measured for the ninth planting (Fig. 1e). In contrast, after the initial irrigation to germinate the wheat seed on DOE 630, several irrigation events occurred and as many as six precipitation events totaling about 5 mm occurred during the sample interval when Φ_s was measured for the 14th planting (Fig. 1f). Warmer temperatures and lower precipitation (Fig. 1) could explain why Φ_s was lower by 0.09 (m³ m⁻³) throughout the 9th (0.24 ± 0.06 m³ m⁻³) compared with the 14th (0.33 ± 0.01 m³ m⁻³) planting.

Over 10 consecutive weeks (five 2-wk sample intervals comparing Heated vs. Reference plots) during the 14th planting meteorological conditions of SR, T_a , and u_a (Fig. 2a), and soil conditions of θ_s and T_s (Fig. 2b) for the most dissimilar (Fig. 2a, 2b) and similar (Fig. 2c, 2d) 3 consecutive days within a week in the Reference plot are illustrated in Fig. 2. On similar days, good agreement was observed among the 3 consecutive days for meteorological conditions of SR and T_a , but greater variation between the most similar 3 consecutive days was observed for u_a (Fig. 2c). Although greater variation was observed for SR and T_a on the 3 most consecutive dissimilar days, u_a was as much as twofold greater on the most dissimilar compared to the most similar 3 consecutive days (Fig. 2a). In contrast, soil conditions of T_s and θ_s , which have the greatest influence on Φ_s , were similar for even the most dissimilar 3 consecutive days in the Reference plot (Fig. 2b, 2d). Consequently, even on the most dissimilar 3 consecutive days, meteorological and especially soil conditions were similar enough to treat days as blocks (replication) in a RCB experimental design.

Infrared Warming

Infrared warming increased the average wheat canopy temperature by 1.3°C during daytime and 2.7°C at nighttime – about 0.2 and 0.3°C below the respective targeted set-points (Wall et al., 2011). Greater deviation from the targeted set-points occurred at midafternoon, because that was when highest wind speeds, atmospheric turbulence, and especially evapotranspiration rates of our well-watered crops occurred.

Microclimate Effects on Midday Soil Temperature and Volumetric Soil-Water Content

Across 10 sampling dates between DOE 649 to 721 (December–March 2008; 14th planting; Fig. 1h), midday (solar noon) T_s in the upper 0.1-m soil depth ranged between 7.8 to 14.6°C in Heated plots and between 6.9 to 13.8°C in Reference plots (Fig. 3a). An ANOVA revealed that mean T_s was greater by 1.6°C in Heated ($11.6 \pm 0.1^\circ\text{C}$) compared with Reference ($10.0 \pm 0.1^\circ\text{C}$) plots (TRT effect; $F_{1,13,9} = 113$; $P < 0.0001$). Repeated measure RTV ($F_{9,28,1} = 5.2$; $P = 0.0004$) and TRT \times RTV interaction ($F_{9,28} = 7.9$; $P < 0.0001$) effects were also detected, because greater difference in T_s between Heated and Reference plots occurred at low θ_s compared to smaller differences at high θ_s after an irrigation or precipitation event rehydrated the soil. An ANOVA by individual sampling date (DOE) revealed that over the majority of the sampling dates, T_s was greater in Heated compared with Reference plots (Fig. 3a).

Across three sampling dates, DOE 380, 394, and 411 (March–April 2008; ninth planting; Fig. 1g), representative

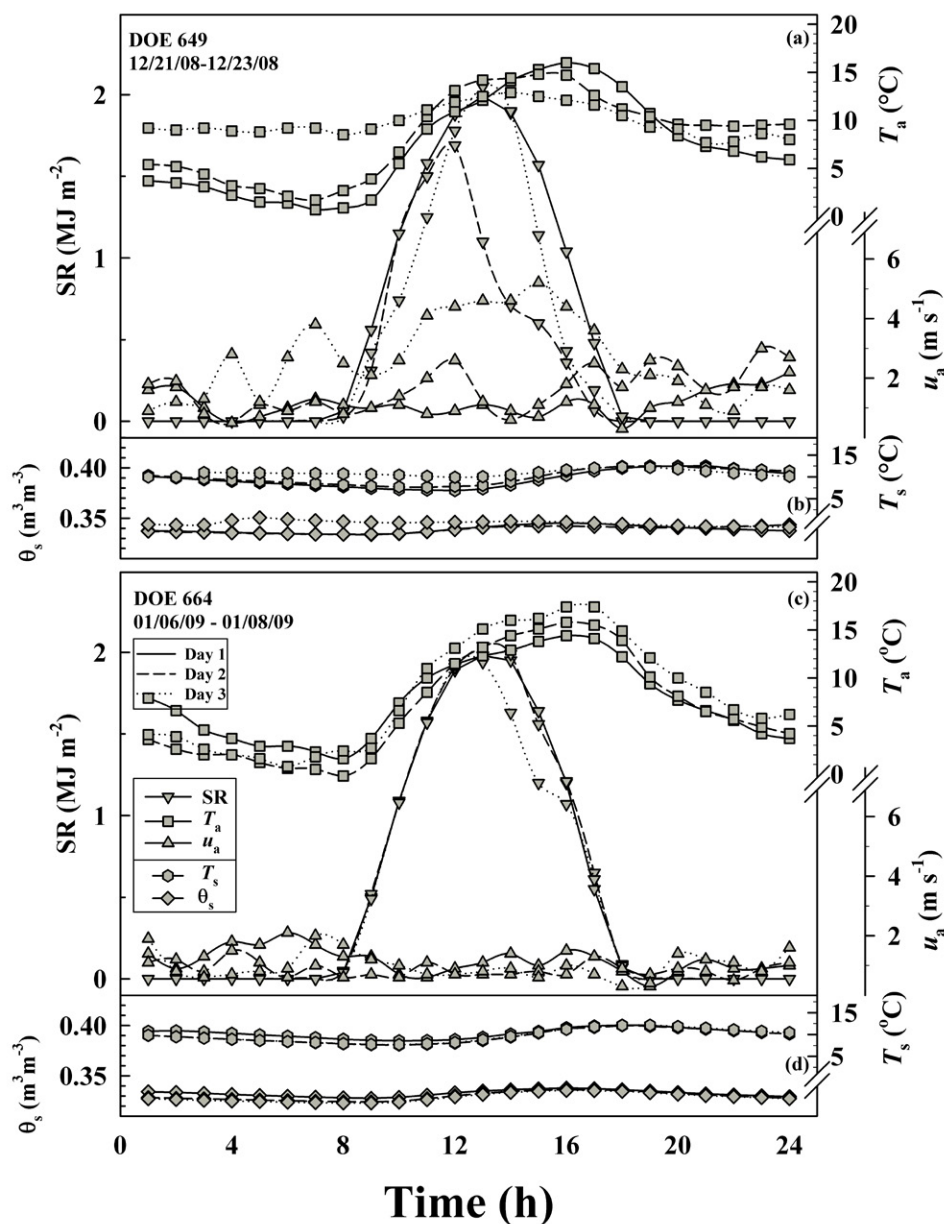


Fig. 2. (a, c) Diel trends in meteorological conditions of incident solar radiation (SR), air temperature (T_a), and wind speed (u_a) at 2-m height, and (b, d) diel soil temperature (T_s) and volumetric soil-water content (θ_s) at 0.1-m depth during 3 consecutive days that had the (a, b) least and (c, d) most similar meteorological and soil conditions for the Reference plot during the 10-wk sample interval (day of experiment [DOE 649 through 715]) when diel soil CO₂ efflux (Φ_s) measurements were measured.

of a warmer than normal temperature regime for a wheat cropping season for the location (March–July), and over the same sampling dates for T_s given above, midday θ_s in the upper 0- to 0.1-m of the soil ranged between 0.17 to 0.36 (m³ m⁻³) in Heated and between 0.24 to 0.36 (m³ m⁻³) in Reference plots (Fig. 3b, 3c). An ANOVA revealed that θ_s was lower by 0.03 (m³ m⁻³) in Heated (0.29 ± 0.02 m³ m⁻³) compared with Reference plots (0.32 ± 0.01 m³ m⁻³) (TRT effect; $F_{1,3.6} = 23.1$; $P = 0.0111$). Repeated measure RTV ($F_{9,18.8} = 17.4$; $P < 0.0001$) and TRT \times RTV interaction ($F_{9,18.8} = 5.6$; $P = 0.0009$) effects were also detected for θ_s , corresponding to consistently lower θ_s in Heated compared with Reference plots as the wheat crop grew. An ANOVA by individual sampling date indicated that initially θ_s was similar between Heated and Reference plots, but that as the wheat

crop grew θ_s decreased in Heated compared with Reference plots (Fig. 3b, 3c). This trend was consistent for both the 9th and 14th plantings (Fig. 3b, 3c). Because higher T_s and lower θ_s were observed in Heated compared with Reference plots, IR warming affected the microclimate (accept Hypothesis 1).

Midday Trends in Soil Carbon Dioxide Efflux

Across 13 sampling dates, midday trends in Φ_s varied systematically (Fig. 3). Overall midday Φ_s was lower for Heated [3.1 ± 0.16 $\mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$] compared with Reference [3.3 ± 0.16 $\mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$] plots (TRT effect; $F_{1,2.0} = 9.5$; $P = 0.0896$) (Fig. 3b, 3c). Nevertheless, repeated measure RTV ($F_{12,30.4} = 8.3$; $P < 0.0001$) and TRT \times RTV interaction ($F_{12,30.4} = 3.5$; $P = 0.0025$) effects were detected. They occurred because as the soil dried from high to low θ_s a

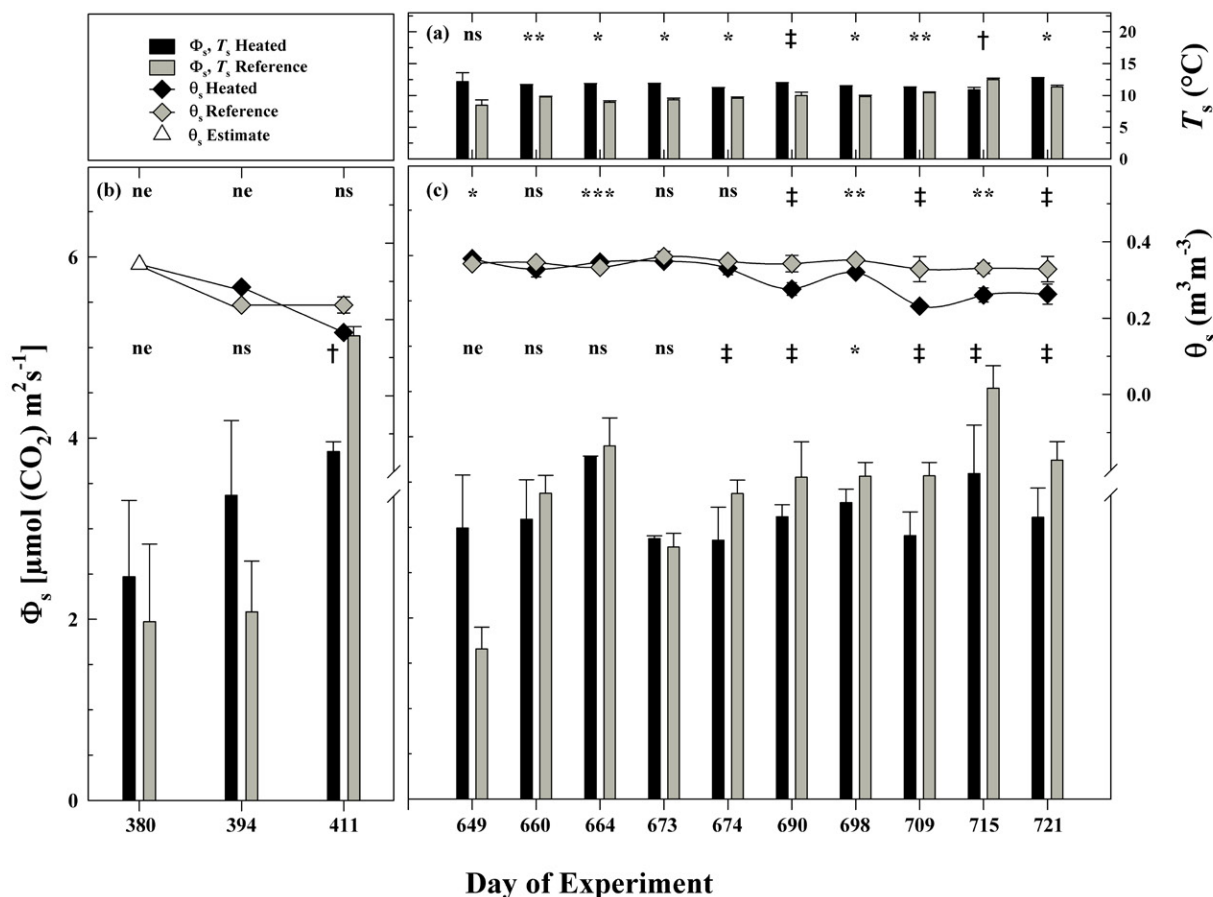


Fig. 3. (a) Midday soil temperature (T_s) for 10 survey sampling dates during the 14th planting of Hot Serial Cereal (HSC) experiment, (b, c) Midday maximum soil CO_2 efflux (Φ_s), and volumetric soil-water content (θ_s) for three sampling dates during the (b) 9th planting, and 10 sampling dates during the (c) 14th planting of the HSC experiment. Significant effects given as *, **, ***, and ns for $P \leq 0.05$, $P \leq 0.01$, $P \leq 0.001$, and not significant, respectively (ne for effect not estimated). Significance also denoted with † and ‡ for $P > 0.05$ and $P \leq 0.1$ and $P > 0.1$ and $P \leq 0.3$, respectively. Each mean datum was derived from three repeated measures across three replications (i.e., $n = 9$). Vertical bars are one standard error of replication mean (i.e., $n = 3$). The above illustration was derived from more than 234 measurements.

treatment inversion occurred for midday Φ_s between Heated and Reference plots. Following an irrigation or precipitation event that rehydrated the soil surface midday Φ_s was greater for Heated compared with Reference plots (DOE 380, 394, 649; Fig. 3b, 3c), but as the soil dried to intermediated levels of θ_s no detectable difference in midday Φ_s was noted between Heated and Reference plots (DOE 664, 673, 674; Fig. 3c), whereas as the soil dried even further at low θ_s midday Φ_s was notable lower for Heated compared with Reference plots (DOE 411, 690, 698, 709, 715, 721; Fig. 3b, 3c) (accept Hypothesis 2).

Diel Trends in Soil Carbon Dioxide Efflux

Across five 2-wk (10 wk) sample intervals (Fig. 4) diel trends in Φ_s exhibited a similar systematic treatment inversion with respect to T_s and θ_s as observed at midday (Fig. 3). Under wet soil conditions at high θ_s diel trends in Φ_s were greater in Heated than Reference plots (DOE 649), but as the soil dried to intermediate levels of θ_s diel trends in Φ_s were similar between Heated and Reference plots (DOE 664, 674), and as the soil dried even further and θ_s decreased in Heated compared with Reference plots diel trends in Φ_s were lower in Heated compared with Reference plots (DOE 698, 715). An almost twofold increase in diel Φ_s was observed between the

first and fifth 2-wk sample interval centered on DOE 649 and 715, respectively (Fig. 4f, 4j).

On DOE 649 (~50% seedling emergence) TOD or TRT \times TOD effects were not detected (Table 1), because diel Φ_s exhibited no distinctive nocturnal or diurnal trend (Fig. 4f). The soil was wet with high θ_s , the intrarow space consisted of bare soil (i.e., heterotrophic respiration), and u_a was high and highly variable (Fig. 4a, 4f). Although diel Φ_s was greater in Heated compared with Reference plots (Fig. 4f), no TRT effect was detected (Table 1). The stepwise reduction in the mixed ANOVA excluded all meteorological (SR, T_a , u_a) and soil (T_s , θ_s) covariates (Table 1).

On DOE 664 (seedling development) TOD and TRT \times TOD effects were detected (Table 1), because diel Φ_s exhibited a distinctive nocturnal and diurnal trend (Fig. 4g). The soil was wet with high θ_s , the intrarow space consisted of mostly bare soil (i.e., heterotrophic respiration), but u_a was low and uniform (Fig. 4b, 4g). The stepwise reduction in the mixed ANOVA detected that the T_a covariate explained most of the variation in diel Φ_s (Table 1). Diel trends in Φ_s followed the thermal-induced effects of SR on T_a during the diurnal period, only to return to a lower baseline during the nocturnal period. A TRT effect was detected (Table 1), because diel Φ_s was lower

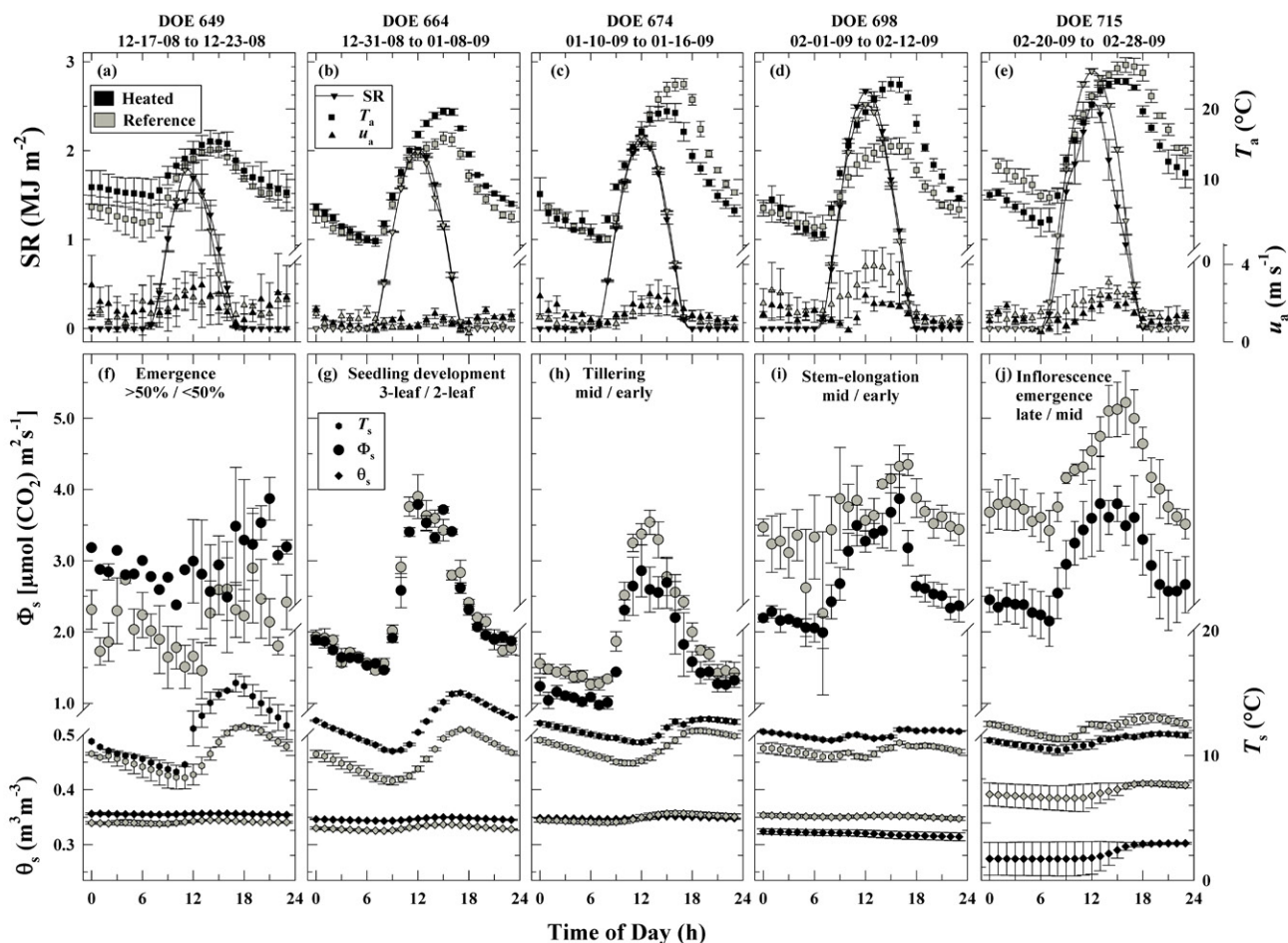


Fig. 4. (a through e) Diel trends in meteorological conditions of incident solar radiation (SR), air temperature (T_a), and wind speed (u_a) at 2-m height, and (f through j) diel soil temperature (T_s) and volumetric soil-water content (θ_s) at 0.1-m depth during five 2-wk intervals centered on day of experiment (DOE) ([a, f] 649, [b, g] 664, [c, h] 674, [d, i] 698, and [e, j] 715) over a 10-wk period when diel soil CO_2 efflux (Φ_s) was measured for Heated and Reference plots (i.e., first week of each 2-wk interval Φ_s measured on Heated plot, second week of each 2-wk interval Φ_s measured on Reference plot). Hourly mean datum was derived from measurement made at a sample frequency of 15 min (i.e., $n = 4$, repeated measure each hour) across the 3 most similar consecutive days (replication), in regards to meteorological and soil conditions, during each week of a 2-wk sample interval (i.e., $n = 12$). Vertical bars are one standard error of replication mean (i.e., $n = 3$). The above illustration was derived from approximately 576 measurements.

in Heated than Reference plots, particularly from dawn until solar noon (Fig. 4g).

On DOE 674 (tillering), TOD and $\text{TRT} \times \text{TOD}$ effects were detected (Table 1), because diel Φ_s exhibited a distinctive nocturnal and diurnal trend (Fig. 4h). The stepwise reduction in the mixed ANOVA detected that the θ_s , T_a , and u_a covariates explained most of the variation in diel Φ_s (Table 1). The soil was drier with slightly lower θ_s in Heated compared with Reference plots, diel trends in Φ_s followed the thermal-induced effects of SR on T_a during the diurnal period only to return to a lower baseline during the nocturnal period, root growth had occurred in the intrarow space (i.e., autotrophic and heterotrophic respiration), and similar to DOE 664 u_a was low and uniform (Fig. 4c, h). A TRT effect was detected because diel Φ_s was lower in Heated compared with Reference plots (Table 1).

Similar to DOE 649, on DOE 698 (stem-elongation) TOD and $\text{TRT} \times \text{TOD}$ effects were not detected (Table 1), because diel Φ_s exhibited only a nominal discernable nocturnal or diurnal trend (Fig. 4i). The soil was drier with reduced θ_s in Heated compared with Reference plots, the root system was

fully developed throughout the intrarow space (i.e., autotrophic and heterotrophic respiration), and u_a was high and highly variable (Fig. 4d, 4i). A TRT effect was detected (Table 1), because diel Φ_s was lower in Heated compared with Reference plots. The T_a and u_a covariates explained most of the variation in diel Φ_s (Table 1).

Similar to DOE 664 and 674, on DOE 715 (inflorescence emergence) TRT and TOD effects were detected (Table 1), because diel Φ_s exhibited a distinctive nocturnal and diurnal trend (Fig. 4j). No $\text{TRT} \times \text{TOD}$ interaction effect was detected (Table 1). The soil had become even drier with a greater reduction in θ_s in Heated compared with Reference plots, the root system was fully developed throughout the intrarow space (i.e., autotrophic and heterotrophic respiration), and u_a was low and uniform (Fig. 4e, 4j). The T_s and SR covariates explained most of the variation in diel Φ_s . This probably occurred because of greater differences in meteorological (SR, T_a , u_a) (Fig. 4e) conditions between the first and second week of the fifth 2-wk interval centered on DOE 715 (Table 1), and could explain why Heated had

lower T_s than Reference plots (Fig. 4j). Nevertheless, the overriding influence of soil drying that reduced θ_s in the Heated compared with Reference plots resulted in a detectable TRT effect (Table 1), because diel Φ_s was lower in the Heated compared with Reference plots (Fig. 4j).

DISCUSSION

Soil organic matter in the agricultural soil was low (~1.2%) and probably consisted mostly of a labile carbon pool of fibrous roots from a previous wheat crop and a more recalcitrant carbon pool. Under bare soil conditions diel Φ_s exhibited a baseline response due predominately to heterotrophic respiration, because of the absence of any actively growing wheat root system in the intrarow soil space. But by canopy closure the wheat crop's root system was fully developed (Wechsung et al., 1995, 1999). As it grew into the intrarow space root/rhizosphere autotrophic respiration contributed to heterotrophic respiration, because an almost twofold increase in Φ_s occurred from bare soil conditions at germination until canopy closure at inflorescence emergence (Fig. 4f through 4j). Diel Φ_s varied systematically and was dependent mostly on soil thermal and moisture regimes consistent with prior reports (Moyano et al., 2012; Suseela et al., 2012).

Infrared warming affected the soil thermal regime. It increased the average wheat canopy temperature by 1.3 and 2.7°C during diurnal and nocturnal periods, respectfully – about 0.2 and 0.3°C below the respective targeted set-points (Wall et al., 2011). Nijs et al. (1996) reported that IR warming maintained a natural temperature gradient of up to 2.5°C offset that of fluctuating ambient air for both the 0.10 and 0.22 m height canopies of *Lolium perenne* L. ('Bastion'), which suggests that IR-warming-based heat transfer was consistent throughout the microclimate. For mixtures of C_3 and C_4 tallgrass prairie grasses Wan et al. (2002) reported that IR warming was relatively uniform over the experimental plots and similar at different soil depths. Heat transfer also appeared to be uniform throughout the microclimate in our wheat study, because soil temperatures were consistently warmer in Heated compared with Reference plots. Hence, the IR-warming-based heat transfer capacity of the T-FACE apparatus was an effective methodology to systematically augment the soil's natural thermal regime under bare soil conditions and as the wheat crop grew. Under ample soil moisture, an exponential increase in Φ_s has been observed with an increase in soil temperatures up to about 40°C in a variety of ecosystems (Lloyd and Taylor, 1994; Janssens and Pilegaard, 2003; Fang and Moncrieff, 2001; Zhou et al., 2009). But in our study on well-watered wheat grown in an agricultural soil, only a modest increase in Φ_s was observed in response to IR warming. Soil CO_2 flux is known to be less sensitive (lower Q_{10}) to temperature variation in arid and semiarid xeric ecosystems with inherently low soil organic matter content (Conant et al., 2000; West and Post, 2002; Zhang et al., 2009; Yuste et al., 2010). The low soil organic matter in the agricultural soil of our study may possibly have limited the magnitude of any thermal response in Φ_s compared to that observed elsewhere. Our sample interval was also limited, because it occurred over a 10-wk interval from germination (bare soil) until inflorescence emergence (canopy

closure) when soil temperatures are normally on the low end of their thermal range for the semiarid desert study region (Fig. 1). For mixtures of C_3 and C_4 tallgrass prairie grasses, Luo et al. (2001) attributed a decrease in the response of Φ_s to IR warming over time to thermal acclimation, noting that the acclimatization was greater at higher soil temperatures. But, substrate limitations and depletion of labile and even recalcitrant carbon pools over time can also explain an observed decrease in Φ_s rather than thermal acclimation of the soil to warmer temperatures (Ågren and Bosatta, 2002; Kirschbaum, 2004; Hartley et al., 2007b; Allison et al., 2010). Soil drying has also been observed to reduce any thermal-based increase in Φ_s in semiarid tallgrass prairie ecosystems (Norman et al., 1992; Conant et al., 2004; Harper et al., 2005).

Infrared warming affected the soil moisture regime. A well-watered soil moisture regime was maintained at constant relative humidity between Heated and Reference plots such as might be expected to occur with global warming (i.e., weekly replacement of evapotranspired water from the Reference plots, whereas the Heated plots received a supplemental irrigation of 10% more than the Reference plots [Kimball, 2005; Wall et al., 2011]). Even with supplemental irrigations, however, over time as the soil dried a systematic decrease in θ_s was observed in Heated compared with Reference plots. Thus, our experimental strategy of providing a supplemental irrigation of 6.3% per degree of warming for Heated compared with Reference plots achieved a modest decrease in soil moisture through the growing seasons as desired to simulate future global warming (Kimball, 2005). Volumetric soil-water content directly affects root and microbial activity and indirectly affects soil physical and chemical properties (Schimel and Clein, 1996; Raich and Schlesinger, 1992). A quadratic response has often been used to characterize the relationship between θ_s and Φ_s (Mielnick and Dugas, 2000). Soil CO_2 efflux is known to reach a maximum around the 50% water holding capacity of the soil, and going toward either the low (dry) or high (wet) ends of the range in θ_s , Φ_s decreases due to lower soil root and microbial respiration. Moisture limitations can induce reductions in plant root respiration and microbial activity, both of which contribute to bulk Φ_s (Zhang et al., 2005). Soil drying can shift bacteria/fungal ratio in favor of fungi (Paul and Clark 1996; Jensen et al., 2003), thereby affecting Φ_s as reported in a companion IR warming study (McLain et al., 2009). Soil CO_2 efflux is known to decrease as the soil dries toward the dry end of θ_s range, because dehydration affects the diffusion of soluble substrates at low θ_s . But as the soil dries from saturation at the wet end, the soil pore size distribution is altered, an effect that can be uneven with depth and could cause a pulse response in Φ_s (Fierer and Schimel, 2003). Such a pulse response in Φ_s also commonly occurs following precipitation events that rehydrate the soil (Liu et al., 2002; Fierer and Schimel, 2003; Huxman et al., 2004; Sponseller, 2007; Chen et al., 2008; Shim et al., 2009). This occurs because precipitation pulses that vary in frequency and intensity trigger biological activity. Hence, antecedent moisture is known to affect ecosystem carbon fluxes in semiarid desert regions (Huxman et al., 2004; Xu et al., 2004; Chen et al., 2008; Shim et al., 2009). Pulse responses in Φ_s could have occurred in our wheat study following irrigation or precipitation events that depleted the soil carbon pool. A decrease in Φ_s occurs as the soil saturates with water (high θ_s) and low

soil air-filled porosity slows the diffusion of oxygen and carbon dioxide. Our wheat crop was well-watered, but the soil generally was not saturated. Anaerobic microsites could have been reduced by IR warming at high θ_s with no detectable effect on Φ_s , but a distinctive reduction in Φ_s occurred at low θ_s as the soil dried.

Clearly, both T_s and θ_s , and their interactive effects were primary factors affecting Φ_s of an agricultural soil in our wheat study. The response of Φ_s to T_s was dependent on θ_s because it increased with T_s , but only under higher levels of θ_s . But, a greater reduction in Φ_s in response to lower θ_s compared to increase in Φ_s in response to increase in T_s was observed. Furthermore, it was often difficult to determine the difference between the effect of T_s and θ_s on Φ_s . Soil CO_2 efflux was responsive to the most limiting factor – either T_s or θ_s . It was relatively insensitive to higher T_s under lower θ_s (Fig. 3 and 4), whereas it was more responsive to higher T_s at higher θ_s (Fig. 3 and 4). Similarly, Φ_s was not as sensitive to θ_s at lower T_s , but it was more responsive to θ_s at higher T_s (Fig. 3 and 4). Warmer canopy temperatures caused greater evapotranspiration rates in Heated compared with Reference plots (Wall et al., 2011). This increased consumptive water use enough between irrigation (including supplemental irrigation for Heated plots) or precipitation events to dry the surface soil layer to a greater degree in Heated compared with Reference plots. Following an irrigation event, therefore, Φ_s may have been more responsive to T_s , because it was greater in Heated compared with Reference plots – pulse response following a precipitation or irrigation event. In the days following an irrigation or precipitation event, however, the uppermost soil layer dried more quickly in Heated compared with Reference plots resulting in a decrease in Φ_s . Furthermore, this treatment inversion in Φ_s in response to IR-warming-induced drying of the soil surface was consistent for both midday and diel Φ_s measurements, and during both warmer and cooler cropping seasons – 9th and 14th plantings (Fig. 3b, 3c), respectively.

Globally the contributions of root-associated processes to Φ_s are estimated to be between 20 and 90% (Boone et al., 1998; Schlesinger and Andrews, 2000) and are about 40% for tallgrass prairie ecosystem (Kucera and Kirkham, 1971). Notwithstanding, a high degree of variance has been observed for Φ_s in native grassland ecosystems on annual, seasonal, and diel scales ranging from reductions, to significant increases, to no response (Liu et al., 2002; Zhou et al., 2007; Xu et al., 2012). Results reported herein are consistent with those reported elsewhere on old-field grassland and tallgrass prairie (Mielnick and Dugas, 2000; Luo et al., 2001; Franzluebbers et al., 2002; Liu et al., 2002; Hartley et al., 2007b; Wan et al., 2007; Shim et al., 2009), cereal grain crops (Buyanovsky et al., 1986; Hartley et al., 2007a; Moyano et al., 2007; Qi et al., 2007), and in other IR warming experiments on an alpine meadow ecotone (Saleska et al., 1999) and semiarid grassland (Luo et al., 2001; Xu et al., 2012). Moyano et al. (2007) suggested that factors controlling Φ_s in a barley (*Hordeum vulgare* L.) agricultural cropping system were comparable to those observed in a native grassland ecosystem, which suggests that results reported herein on wheat grown in a semiarid desert region are applicable to other mesic and xeric ecosystems. The high variability in the response of Φ_s to T_s and θ_s suggest that a more complex mechanism is required to determine their

interactive effects. Hence, to elucidate accurate predictions of Φ_s in response to global warming the interactive effect of T_s and θ_s need to be coupled (Mielnick and Dugas, 2000).

CONCLUSIONS

Infrared warming with T-FACE is an effective methodology to investigate the impact of global warming on Φ_s in an agricultural soil. Noteworthy conclusions from our study include the following: (i) IR warming increased T_s and decreased θ_s ; (ii) IR warming initially increased Φ_s following soil hydration, but as the soil surface dried, Φ_s decreased even under warmer T_s . The observed changes in Φ_s in response to θ_s and T_s reported herein are consistent in both magnitude and direction as those in prior literature reports. In short, those regions of the Earth that contain high soil carbon substrate that become wetter in the future will likely exhibit an increase in Φ_s , but with greater drying predicted for many semiarid desert regions that contain low soil carbon substrate Φ_s is likely to decrease even as the Earth becomes warmer.

REFERENCES

- Ågren, G.I., and E. Bosatta. 2002. Reconciling differences in predictions of temperature response of soil organic matter. *Soil Biol. Biochem.* 34:129–132. doi:10.1016/S0038-0717(01)00156-0
- Allison, S.D., M.D. Wallenstein, and M.A. Bradford. 2010. Soil-carbon response to warming dependent on microbial physiology. *Nat. Geosci.* 3:336–340. doi:10.1038/ngeo846
- Bond-Lamberty, B., C.K. Wang, and S.T. Gower. 2004. A global relationship between the heterotrophic and autotrophic components of soil respiration? *Glob. Change Biol.* 10:1756–1766. doi:10.1111/j.1365-2486.2004.00816.x
- Boone, R.D., K.J. Nadelhoffer, J.D. Canary, and J.P. Kaye. 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration. *Nature (London)* 396:570–572. doi:10.1038/25119
- Box, G.E.P., W.G. Hunter, and J.S. Hunter. 1978. *Statistics for experimenters: An introduction to design, data analysis and model building*. John Wiley & Sons, New York.
- Buyanovsky, G.A., G.H. Wagner, and C.J. Gantzer. 1986. Soil respiration in a winter wheat ecosystem. *Soil Sci. Soc. Am. J.* 50:338–344. doi:10.2136/sssaj1986.03615995005000020017x
- Chen, S., G. Lin, J. Huang, and M. He. 2008. Responses of soil respiration to simulated precipitation pulses in semiarid steppe under different grazing regimes. *J. Plant Ecol.* 1:237–246. doi:10.1093/jpe/rtn020
- Conant, R.T., P. Dalla-Betta, C.C. Klopatek, and J.M. Klopatek. 2004. Controls on soil respiration in semiarid soils. *Soil Biol. Biochem.* 36:945–951. doi:10.1016/j.soilbio.2004.02.013
- Conant, R.T., J.M. Klopatek, and C.C. Klopatek. 2000. Environmental factors controlling soil respiration in three semiarid ecosystems. *Soil Sci. Soc. Am. J.* 64:383–390. doi:10.2136/sssaj2000.641383x
- Davidson, E.A., E. Belk, and R.D. Boone. 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Glob. Change Biol.* 4:217–227. doi:10.1046/j.1365-2486.1998.00128.x
- Davidson, E.A., S.E. Trumbore, and R. Amundson. 2000. Soil warming and organic carbon content. *Nature (London)* 408:789–790. doi:10.1038/35048672
- Eswaran, H., E. Van Den Berg, and P. Reich. 1993. Organic carbon in soils of the world. *Soil Sci. Soc. Am. J.* 57:192–194. doi:10.2136/sssaj1993.03615995005700010034x
- Fang, C., and J.B. Moncrieff. 2001. The dependence of soil CO_2 efflux on temperature. *Soil Biol. Biochem.* 33:155–165. doi:10.1016/S0038-0717(00)00125-5
- Fierer, N., and J.P. Schimel. 2002. Effects of drying-rewetting frequency on soil carbon and nitrogen transformations. *Soil Biol. Biochem.* 34:777–787. doi:10.1016/S0038-0717(02)00007-X
- Fierer, N., and J.P. Schimel. 2003. A proposed mechanism for the pulse in carbon dioxide production commonly observed following the rapid rewetting of dry soil. *Soil Sci. Soc. Am. J.* 67:798–805. doi:10.2136/sssaj2003.0798

- Franzluebbers, K., A.J. Franzluebbers, and M.D. Jawson. 2002. Environmental controls on soil and whole-ecosystem respiration from a tallgrass prairie. *Soil Sci. Soc. Am. J.* 66:254–262. doi:10.2136/sssaj2002.0254
- Hanson, P.J., N.T. Edwards, C.T. Garten, and J.A. Andrews. 2000. Separating root and soil microbial contributions to soil respiration: A review of methods and observations. *Biogeochemistry* 48:115–146. doi:10.1023/A:1006244819642
- Harper, C.W., J.M. Blair, P.A. Fay, A.K. Knapp, and J.D. Carlisle. 2005. Increased rainfall variability and reduced rainfall amount decreases soil CO₂ flux in a grassland ecosystem. *Glob. Change Biol.* 11:322–334. doi:10.1111/j.1365-2486.2005.00899.x
- Harte, J., and R. Shaw. 1995. Shifting dominance within a montane vegetation community: Results of a climate-warming experiment. *Science* (Washington, DC) 267:876–880. doi:10.1126/science.267.5199.876
- Harte, J., M.S. Torn, F.-R. Chang, B. Feifarek, A.P. Kinzig, R. Shaw, and K. Shen. 1995. Global warming and soil microclimate: Results from a meadow-warming experiment. *Ecol. Appl.* 5:132–150. doi:10.2307/1942058
- Hartley, I.P., A. Heinemeyer, S.P. Evans, and P. Ineson. 2007a. The effects of soil warming on bulk soil vs. rhizosphere respiration. *Glob. Change Biol.* 13:2654–2667. doi:10.1111/j.1365-2486.2007.01454.x
- Hartley, I.P., A. Heinemeyer, and P. Ineson. 2007b. Effects of three years of soil warming and shading on the rate of soil respiration: Substrate availability and not thermal acclimation mediates observed responses. *Glob. Change Biol.* 13:1786–1797. doi:10.1111/j.1365-2486.2007.01383.x
- Hibbard, K.A., B.E. Law, M. Reichstein, and J. Sulzman. 2005. An analysis of soil respiration across northern hemisphere temperate ecosystems. *Biogeochemistry* 73:29–70. doi:10.1007/s10533-004-2946-0
- Hungate, B.A., K.-J. van Groenigen, J. Six, J.D. Jastrow, Y. Luo, M.-A. de Graaff et al. 2009. Assessing the effect of elevated carbon dioxide on soil carbon: A comparison of four meta-analyses. *Glob. Change Biol.* 15:2020–2034. doi:10.1111/j.1365-2486.2009.01866.x
- Hütsch, B., A. Jürgen, and W. Merbach. 2002. Plant rhizodeposition: an important source of carbon turnover in soils. *J. Plant Nutr. Soil Sci.* 165:397–407. doi:10.1002/1522-2624(200208)165:4<397::AID-JPLN397>3.0.CO;2-C
- Huxman, T.E., K.A. Snyder, D. Tissue, A.J. Leffler, K. Ogle, W.T. Pockman et al. 2004. Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia* 141:254–268. doi:10.1007/s00442-004-1682-4
- IPCC. 2007. Climate Change 2007: The physical science basis. Contribution of Working Group I to the fourth assessment report of the intergovernmental panel on climate change. S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, and H.L. Miller, editors. Cambridge Univ. Press, New York.
- Janssens, I.A., and K. Pilegaard. 2003. Large seasonal changes in Q₁₀ of soil respiration in a beech forest. *Glob. Change Biol.* 9:911–918. doi:10.1046/j.1365-2486.2003.00636.x
- Jensen, K.D., C. Beier, A. Michelsen, and B.A. Emmett. 2003. Effects of experimental drought on microbial processes in two temperate heathlands at contrasting water conditions. *Appl. Soil Ecol.* 24:165–176. doi:10.1016/S0929-1393(03)00091-X
- Kimball, B.A. 2005. Theory and performance of an infrared heater for ecosystem warming. *Glob. Change Biol.* 11:2041–2056. doi:10.1111/j.1365-2486.2005.01028.x
- Kimball, B.A., M.M. Conley, S. Wang, X. Lin, C. Luo, J. Morgan, and D. Smith. 2008. Infrared heater arrays for warming ecosystem field plots. *Glob. Change Biol.* 14:309–320. doi:10.1111/j.1365-2486.2007.01486.x
- Kirschbaum, M.U.F. 1995. The temperature dependence of soil organic matter decomposition and the effects of global warming on soil organic C storage. *Soil Biol. Biochem.* 27:753–760. doi:10.1016/0038-0717(94)00242-S
- Kirschbaum, M.U.F. 2000. Will changes in soil organic carbon act as a positive or negative feedback on global warming? *Biogeochemistry* 48:21–51. doi:10.1023/A:1006238902976
- Kirschbaum, M.U.F. 2004. Soil respiration under prolonged soil warming: Are rate reductions caused by acclimation or substrate loss? *Glob. Change Biol.* 10:1870–1877. doi:10.1111/j.1365-2486.2004.00852.x
- Kucera, C.L., and D.R. Kirkham. 1971. Soil respiration studies in tallgrass prairie in Missouri. *Ecology* 52:912–915. doi:10.2307/1936043
- Kuzyakov, Y. 2006. Sources of CO₂ efflux from soil and review of partitioning methods. *Soil Biol. Biochem.* 38:425–448. doi:10.1016/j.soilbio.2005.08.020
- Littell, R.C., G.A. Milliken, W.W. Stroup, and R.D. Wolfinger. 1996. SAS system for mixed models. SAS Inst., Cary, NC.
- Liu, X., S. Wan, B. Su, D. Hui, and Y. Luo. 2002. Response of soil CO₂ efflux to water manipulation in a tallgrass prairie ecosystem. *Plant Soil* 240:213–223. doi:10.1023/A:1015744126533
- Lloyd, J., and J.A. Taylor. 1994. On the temperature dependence of soil respiration. *Funct. Ecol.* 8:315–323. doi:10.2307/2389824
- Luo, Y.Q., S.Q. Wan, D.F. Hui, and L.L. Wallace. 2001. Acclimatization of soil respiration to warming in a tall grass prairie. *Nature* (London) 413:622–625. doi:10.1038/35098065
- Luo, C., G. Xu, Z. Chao, S. Wang, X. Lin, Y. Hu et al. 2010. Effect of warming and grazing on litter mass loss and temperature sensitivity of litter and dung mass loss on the Tibetan plateau. *Glob. Change Biol.* 16:1606–1617. doi:10.1111/j.1365-2486.2009.02026.x
- McLain, J.E.T., G.W. Wall, B.A. Kimball, J.W. White, and M.J. Ottman. 2009. Using real-time quantitative PCR to examine the dynamics of soil fungi and bacteria in response to ecosystem warming. [CD] ASA, CSSA, and SSSA, Madison, WI.
- Melillo, J.M., P.A. Steudler, J.D. Aber, K. Newkirk, H. Lux, F.P. Bowles et al. 2002. Soil warming and carbon-cycle feedbacks to the climate system. *Science* (Washington, DC) 298:2173–2176. doi:10.1126/science.1074153
- Mielnick, P.C., and W.A. Dugas. 2000. Soils CO₂ flux in a tallgrass prairie. *Soil Biol. Biochem.* 32:221–228. doi:10.1016/S0038-0717(99)00150-9
- Morgan, J.A., D.R. LeCain, E. Pendall, D.M. Blumenthal, B.A. Kimball, Y. Carrillo et al. 2011. C₄ grasses prosper as carbon dioxide eliminates desiccation in warmed semi-arid grassland. *Nature* (London) 476:202–206. doi:10.1038/nature10274
- Moyano, F.E., W.L. Kutsch, and E.-D. Schulze. 2007. Response of mycorrhizal, rhizosphere and soil basal respiration to temperature and photosynthesis in a barley field. *Soil Biol. Biochem.* 39:843–853. doi:10.1016/j.soilbio.2006.10.001
- Moyano, F.E., N. Vasilyeva, L. Bouckaert, F. Cook, J. Craine, J.C. Yuste et al. 2012. The moisture response of soil heterotrophic respiration: Interaction with soil properties. *Biogeosciences* 9:1173–1182. doi:10.5194/bg-9-1173-2012
- Nijs, I., F. Kockelbergh, H. Teughels, H. Blum, G. Hendrey, and I. Impens. 1996. Free Air Temperature Increase (FATI): A new tool to study global warming effects on plants in the field. *Plant Cell Environ.* 19:495–502. doi:10.1111/j.1365-3040.1996.tb00343.x
- Niu, S., Z. Li, J. Xia, Y. Han, M. Wu, and S. Wan. 2008. Climatic warming changes plant photosynthesis and its temperature dependence in a temperate steppe of northern China. *Environ. Exp. Bot.* 63:91–101. doi:10.1016/j.envexpbot.2007.10.016
- Norman, J.M., R. Garcia, and S.B. Verma. 1992. Soil surface CO₂ fluxes and the carbon budget of a grassland. *G Biogeosci.* 97:18845–18853. doi:10.1029/92JD01348.
- Ottman, M.J., B.A. Kimball, J.W. White, and G.W. Wall. 2012. Wheat growth response to increased temperature from varied planting dates and supplemental infrared heating. *Agron. J.* 104:7–16. doi:10.2134/agronj2011.0212
- Parton, W.J., J.A. Morgan, G. Wang, and S. Del Grosso. 2007. Projected ecosystem impact of the prairie heating and CO₂ enrichment experiment. *New Phytol.* 174:823–834. doi:10.1111/j.1469-8137.2007.02052.x
- Paul, E.A., and F.E. Clark. 1996. Soil microbiology and biochemistry. 2nd ed. Academic Press, San Diego, CA.
- Qi, Y.-C., Y.-S. Dong, J.-Y. Liu, M. Domroes, Y.-B. Geng, L.-X. Liu et al. 2007. Effect of the conversion of grassland to spring wheat field on the CO₂ emission characteristics in inner Mongolia, China. *Soil Tillage Res.* 94:310–320. doi:10.1016/j.still.2006.08.008
- Raich, J.W., and K.J. Nadelhoffer. 1989. Belowground carbon allocation in forest ecosystems: Global trends. *Ecology* 70:1346–1354. doi:10.2307/1938194
- Raich, J.W., and C.S. Potter. 1995. Global patterns of carbon dioxide emissions from soil. *Global Biogeochem. Cycles* 9:23–26. doi:10.1029/94GB02723
- Raich, J.W., C.S. Potter, and D. Bhawagati. 2002. Interannual variability in global soil respiration. *Glob. Change Biol.* 8:800–812. doi:10.1046/j.1365-2486.2002.00511.x
- Raich, J.W., and W.H. Schlesinger. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus B.* 44:81–99. doi:10.1034/j.1600-0889.1992.t011-1-00001.x
- Raich, J.W., and A. Tufekcioglu. 2000. Vegetation and soil respiration: Correlation and controls. *Biogeochemistry* 48:71–90. doi:10.1023/A:1006112000616

- Rustad, L.E., J.L. Campbell, G.M. Marion, R.J. Norby, M.J. Mitchell, A.E. Hartley et al. 2001. A meta analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* 126:543–562. doi:10.1007/s004420000544
- Rustad, L.E., T.G. Huntington, and R.D. Boone. 2000. Controls on soil respiration: Implications for climate change. *Biogeochemistry* 48:1–6. doi:10.1023/A:1006255431298
- Saleska, S.R., J. Harte, and M.S. Torn. 1999. The effect of experimental ecosystem warming on CO₂ fluxes in a montane meadow. *Glob. Change Biol.* 5:125–141. doi:10.1046/j.1365-2486.1999.00216.x
- SAS Institute. 2009. SAS/STAT® 9.2 User's guide. 2nd ed. SAS Inst., Cary, NC.
- Schimel, J.P., and J.S. Clein. 1996. Microbial response to freeze-thaw cycles in tundra and taiga soils. *Soil Biol. Biochem.* 28:1061–1066. doi:10.1016/0038-0717(96)00083-1
- Schindlbacher, A., S. Zechmeister-Boltenstern, and R. Jandl. 2009. Carbon losses due to soil warming: Do autotrophic and heterotrophic soil respiration respond equally? *Glob. Change Biol.* 15:901–913. doi:10.1111/j.1365-2486.2008.01757.x
- Schlesinger, W.H., and J.A. Andrews. 2000. Soil respiration and the global carbon cycle. *Biogeochemistry* 48:7–20. doi:10.1023/A:1006247623877
- Shaw, M.R., and J. Harte. 2001. Response of nitrogen cycling to simulated climate change: Differential responses along a subalpine ecotone. *Glob. Change Biol.* 7:193–210. doi:10.1046/j.1365-2486.2001.00390.x
- Shen, W., G.D. Jenerette, D. Hui, R.P. Phillips, and H. Ren. 2008. Effects of changing precipitation regimes on dryland soil respiration and C pool dynamics at rainfall event, seasonal and interannual scales. *J. Geophys. Res.* 113:G03024. doi:10.1029/2008JG000685
- Shen, W., J.F. Reynolds, and D. Hui. 2009. Responses of dryland soil respiration and soil carbon pool size to abrupt vs. gradual and individual vs. combined changes in soil temperature, precipitation, and atmospheric [CO₂]: A simulation analysis. *Glob. Change Biol.* 15:2274–2294. doi:10.1111/j.1365-2486.2009.01857.x
- Shim, J.H., E. Pendall, J.A. Morgan, and D.S. Ojima. 2009. Wetting and drying cycles drive variations in the stable carbon isotope ratio of respired carbon dioxide in semi-arid grassland. *Oecologia* 160:321–333. doi:10.1007/s00442-009-1302-4
- Singh, B.K., L.A. Dawson, C.A. Macdonald, and S.M. Buckland. 2009. Impact of biotic and abiotic interaction on soil microbial communities and functions: A field study. *Appl. Soil Ecol.* 41:239–248. doi:10.1016/j.apsoil.2008.10.003
- Sponseller, R.A. 2007. Precipitation pulses and soil CO₂ flux in a Sonoran Desert ecosystem. *Glob. Change Biol.* 13:426–436. doi:10.1111/j.1365-2486.2006.01307.x
- Subke, J.-A., I. Inglisma, and M.F. Cotrufo. 2006. Trends and methodological impacts in soil CO₂ efflux partitioning: A metaanalytical review. *Glob. Change Biol.* 12:921–943. doi:10.1111/j.1365-2486.2006.01117.x
- Suseela, V., R.T. Conant, M.D. Wallenstein, and J.S. Dukes. 2012. Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change experiment. *Glob. Change Biol.* 18:336–348. doi:10.1111/j.1365-2486.2011.02516.x
- Taylor, J.A., and J. Lloyd. 1992. Sources and sinks of atmospheric CO₂. *Aust. J. Bot.* 40:407–418. doi:10.1071/BT9920407
- Torn, M.S., and J. Harte. 1996. Methane consumption by montane soils: Implications for positive and negative feedback with climatic change. *Biogeochemistry* 32:53–67. doi:10.1007/BF00001532
- Wall, G.W., B.A. Kimball, J.W. White, and M.J. Ottman. 2011. Gas exchange and water relations responses of spring wheat to full-season infrared warming. *Glob. Change Biol.* 17:2113–2133. doi:10.1111/j.1365-2486.2011.02399.x
- Wan, S., and Y. Luo. 2003. Substrate regulation of soil respiration in a tall-grass prairie: Results of a clipping and shading experiment. *Global Biogeochem. Cycles* 17:1054. doi:10.1029/2002GB001971
- Wan, S., Y. Luo, and L.L. Wallace. 2002. Changes in microclimate induced by experimental warming and clipping in tallgrass prairie. *Glob. Change Biol.* 8:754–768. doi:10.1046/j.1365-2486.2002.00510.x
- Wan, S., R.J. Norby, J. Ledford, and J.F. Weltzini. 2007. Responses of soil respiration to elevated CO₂, air warming, and changing soil water availability in a model old-field grassland. *Glob. Change Biol.* 13:2411–2424. doi:10.1111/j.1365-2486.2007.01433.x
- Wan, S., J. Xia, W. Liu, and S. Niu. 2009. Photosynthetic over-compensation under nocturnal warming enhances grassland carbon sequestration. *Ecology* 90:2700–2710. doi:10.1890/08-2026.1
- Wechsung, G., F. Wechsung, G.W. Wall, F.J. Adamsen, B.A. Kimball, R.L. Garcia et al. 1995. Biomass and growth rate of a spring wheat root system grown in Free-Air CO₂ Enrichment (FACE) and ample soil moisture. *J. Biogeogr.* 22:623–634. doi:10.2307/2845963
- Wechsung, G., F. Wechsung, G.W. Wall, F.J. Adamsen, B.A. Kimball, P.J. Pinter, Jr., et al. 1999. The effects of free-air CO₂ enrichment and soil water availability on spatial and seasonal patterns of wheat root growth. *Glob. Change Biol.* 5:519–529. doi:10.1046/j.1365-2486.1999.00243.x
- West, T.O., and W.M. Post. 2002. Soil organic carbon sequestration rates by tillage and crop rotation: A global data analysis. *Soil Sci. Soc. Am. J.* 66:1930–1946. doi:10.2136/sssaj2002.1930
- Xia, J., Y. Han, Z. Zhang, Z. Zhang, and S. Wan. 2009. Effects of diurnal warming on soil respiration are not equal to the summed effects of day and night warming in a temperate steppe. *Biogeosciences* 6:1361–1370. doi:10.5194/bg-6-1361-2009
- Xu, L., D.D. Baldocchi, and J. Tang. 2004. How soil moisture, rain pulses, and growth alter the response of ecosystem respiration to temperature. *Global Biogeochem. Cycles* 18:GB4002. doi:10.1029/2004GB002281
- Xu, X., R.A. Sherry, S. Niu, J. Zhou, and Y. Luo. 2012. Long-term experimental warming decreased labile soil organic carbon in a tallgrass prairie. *Plant Soil* 361:307–315. doi:10.1007/s11104-012-1265-9
- Yuste, J.C., S. Ma, and D.D. Baldocchi. 2010. Plant-soil interactions and acclimation to temperature of microbial-mediated soil respiration may affect predictions of soil CO₂ efflux. *Biogeochemistry* 98:127–138. doi:10.1007/s10533-009-9381-1
- Zhang, L., Y. Chen, W. Li, and R. Zhao. 2009. Abiotic regulators of soil respiration in desert ecosystems. *Environ. Geol.* 57:1855–1864. doi:10.1007/s00254-008-1474-y
- Zhang, W., K.M. Parker, Y. Luo, S. Wan, L.L. Wallace, and S. Hu. 2005. Soil microbial responses to experimental warming and clipping in a tallgrass prairie. *Glob. Change Biol.* 11:266–277. doi:10.1111/j.1365-2486.2005.00902.x
- Zhou, T., P. Shi, D. Hui, and Y. Luo. 2009. Global pattern of temperature sensitivity of soil heterotrophic respiration (Q₁₀) and its implications for carbon-climate feedback. *J. Geophys. Res.* 114:G02016. doi:10.1029/2008JG000850
- Zhou, X., S. Wan, and Y. Luo. 2007. Source components and interannual variability of soil CO₂ efflux under experimental warming and clipping in a grassland ecosystem. *Glob. Change Biol.* 13:761–775. doi:10.1111/j.1365-2486.2007.01333.x